A STUDY OF THE ELLIPTICAL GOLDENROD GALL CAUSED BY GNORIMOSCHEMA GALLÆSOLIDAGINIS RILEY

By George W. Barber

Associate Entomologist, Bureau of Entomology and Plant Quarantine, United States Department of Agriculture

INTRODUCTION

The insects, beset on every hand in nature by enemies—animal and plant, predacious and parasitic, and dependent upon the vicissitudes of the physical environment, have developed many interesting, surprising, and curious means of protection against these decimating factors. Few of the protective adaptations are more wonderful or less understood than those of the gall-forming insects, which, by one means or another, cause the host plants to build them habitations out of their plant substance, wherein the insects may feed in comparative security.

A host of insect species attacking many species of plants cause galls to develop on roots, stems, branches, twigs, leaves, or other parts, and they frequently become numerous enough to cause severe injury to the plants attacked. These galls form one of the curiosities of any countryside, sure to attract the attention of the naturalist.

While the galls of some insects are very elaborate in structure, one of the simplest may take the form of a more or less pronounced swelling of the stem, resulting from feeding by the insect therein. Some of the galls inhabited by the gelechiid moth *Gnorimoschema gallæsolidaginis* Riley appear to be of this type, the stem being hollowed out for a certain distance vertically and but little swollen. Other individuals of this species inhabit better defined galls that are sometimes nearly or quite globular.

For years the writer has observed these goldenrod galls in various localities and has been interested in the variation that they showed, but he had not found them in numbers sufficient for a study of this variation. However, in 1929, in a locality near Richmond, Va., a large infestation of the insect was observed. In one roadside spot every second or third stalk of goldenrod bore one or more galls of this species, and a sufficient number could be obtained for study. Since these galls varied greatly in size, an effort was made to determine the probable reason for the variation, whether it extended to the insects inhabiting the galls, and in what way such variations were related. A further effort was made to determine what degree of protection the gall formation afforded the insect habitant.

HABITS AND LIFE HISTORY OF THE GALL MAKER

In central Virginia the galls begin to appear on the partly grown goldenrod plants late in June or in July, but development of the insect within the galls is slow. By the middle of August the larvæ become full grown and begin to pupate, and the moths emerge during October, there being a single generation annually. Leiby[1] found that the eggs of *G. gallæsolidaginis* are deposited in the fall on goldenrod stems or leaves. These hatch the following spring, and the young larvæ migrate to new goldenrod shoots in the vicinity, crawl to the buds, enter them from the side, and bore downward in the stems for a short distance. Here the larvæ settle and feed on the inner walls of their burrows. The progress of emergence in the autumn of 1929 is indicated by the following records: From the 1st to the 4th of September 2,000 galls were collected but from none of them had the moths emerged; on September 30, when 500 galls were collected, moths had emerged from only 2.6 per cent of them; on October 15 and November 5, however, from 500 galls collected on each date, moths had emerged from 39.8 per cent and 100 per cent, respectively.

During the time that the larva is feeding, no opening is seen in the gall and no communication with the outside is apparent. While this condition is admirably suited to the needs of the larva, as it permits the latter to feed and grow unhurried by fear of danger, this shelter, unless there were special provision for escape from it, would prove to be a tomb for the moth, which lacks suitable mouthparts for biting through the plant tissue forming the gall. Providing for the escape of the moth is the last act of the larva

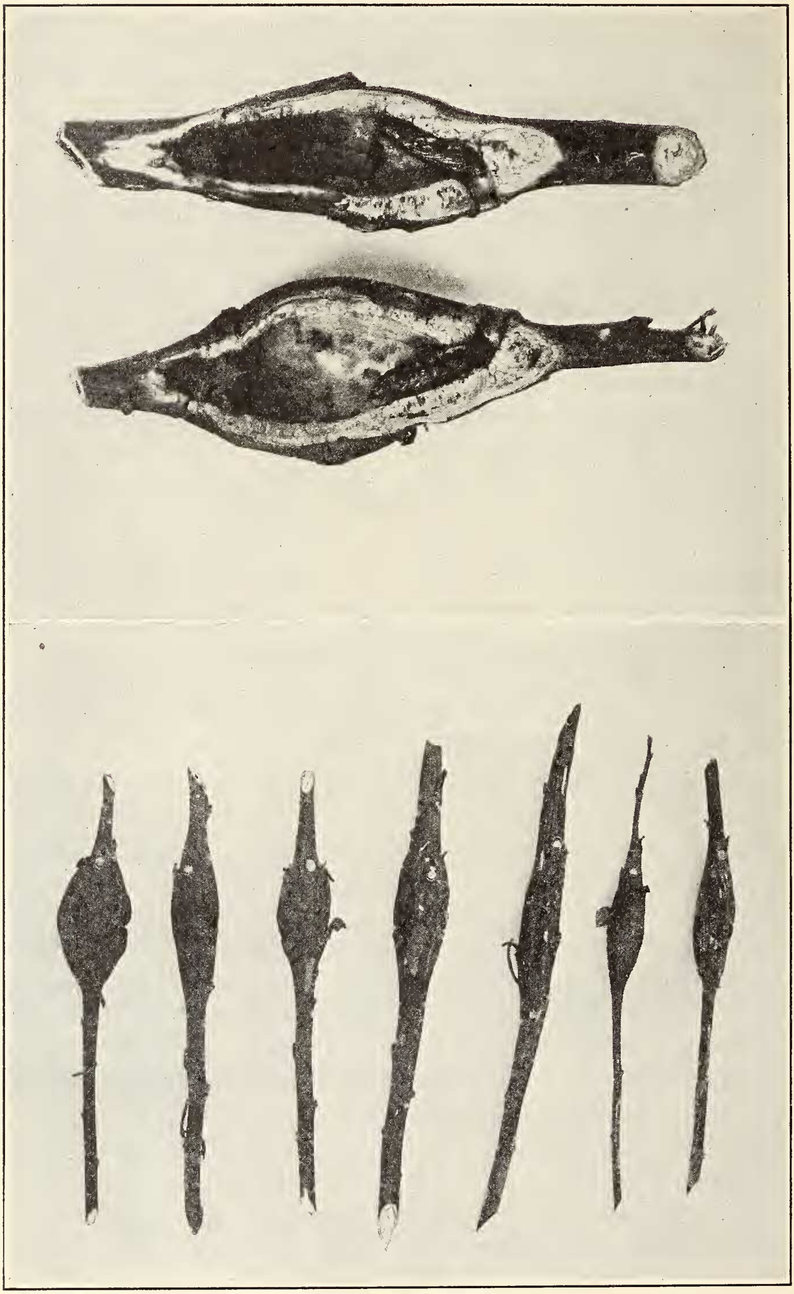
[1] Leiby, R. W., Biology of the goldenrod gall-maker *Gnorimoschema gallæsolidaginis* Riley. Jour. N. Y. Ent. Soc. 30: 81–94, lilus. 1922.

before pupating, and this provision is perhaps among the most remarkable to be found among insects.

The larva, which seemingly feeds upon the inner wall of the gall, maintains a neat and thoroughly sanitary habitation. All fecal matter is deposited in the bottom of the gall and covered with silk. When the larva is through feeding, a heavier layer of silk is applied to the piled fecal matter and to the entire inner surface of the gall. A tunnel is now gnawed from the uppermost point in the gall toward the outside, not entirely through the wall, as usually described in literature, but only partly through. To leave the burrow open, or even covered with silk, would expose the retiring insect to too great danger from enemies that could easily enter. Some time before the burrow has reached the surface, the larva discontinues gnawing, covers the burrow with silk continuous with that laid down on the inner wall of the gall, and proceeds to the most delicate task of its life. It cuts a groove continuous with the wall of the burrow, through to the outside of the gall, leaving undisturbed the contained circular section of the wall. The groove is directed slightly away from the center as the outer surface of the gall is approached, making the diameter of the carved-out cylinder to increase from within outward. The resulting plug is entirely severed from the surrounding wall of the gall, and the groove appears on the outside as a circle.

The last detail of its chamber having been completed, the larva retires to the hollow of the gall to pupate. The emergence burrow is securely closed by a structure which is a true "bung," entirely separated from the rest of the wall of the gall. From the inside a mere touch will force the plug out of the emergence burrow, but it cannot be forced in from the outside except by considerable pressure. Frequently, as the plant ripens and the stalk dries, the plug assumes a lighter color than the surface of the gall proper and is easily seen, as in figure 2. Enough light enters through the groove separating the plug from the gall to direct the moth toward the avenue of escape provided for it.

The plug, or "stopper," was always present in galls containing pupæ, and it was always suitable for the emergence of the moths; for in no case, among the hundreds of examples of the gall studied, did a moth fail to gain freedom by this means. (Fig. 1.)



Above—FIGURE 1.—Goldenrod galls split to show hollow interior, the piled excrement at the base, the emergence plug, and the pupæ. *Below*—FIGURE 2.—A series of goldenrod galls showing the position and discoloration of the plugs.

Among insects, prescience in the provision by one stage for the welfare of a succeeding stage is a common enough phenomenon, but in this instance the arrangements are much more complete than usual. Many boring insects make provision in the larval stage for the escape of the mature insect. In the goldenrod ball gall, caused by the trypetid fly *Eurosta solidaginis* Fitch, the maggot occupies a small cell surrounded by a greatly thickened wall. The insect passes the winter as a full grown maggot within the gall, no provision having been made thus far for the emergence of the delicate fly. In spring an emergence burrow is constructed by the maggot which leaves intact a thin cap partially cut through the outer wall of the gall. This the fly is able to push away as it seeks its freedom.

Among Lepidoptera, the full grown larva of *Diatræa crambidoides* Grote bores to the lowest point in the stalk of the corn plant in which it has fed, and here, some distance below the surface of the soil, it hibernates. In spring the larva becomes active, retraces its burrow, or gnaws a new one upward through the stalk to a point a few inches above the surface of the soil, and there gnaws an opening through the wall of the stalk to the outside, closes the opening with silk as a protection, and retires to pupate.

These two examples illustrate the usual way in which many larvæ feeding in the interior of plants provide for the escape of the adults. As compared with *Eurosta* or *Diatræa*, it may be seen that *Gnorimoschema* constructs a protective device that is a great step forward. When the adults are provided with biting mouth parts, as in the case of some of the true gall wasps, no provision is made by the larvæ at all, since the adults are able to shift for themselves.

PROBABLE CAUSE OF THE GALL

The following theories regarding gall formation by insects have been advanced: (1) That the gall results from mechanical irritation to the plant parts caused by the feeding of the insect; (2) that the gall results from the introduction of specific chemical substances by the insect; (3) that the gall structure results from stimulation induced by the by-products of body metabolism—urea and carbon dioxide—of the gall insect; (4) that the gall is produced as protective tissue for the purpose of isolating in a cell the foreign body, the gall insect, and thus is a structure beneficial to the injured plant. With the insect under discussion, the first theory is the one held to be most probable.

VARIATION

The plants bearing galls were variable in size, some being only 5 or 6 inches tall whereas others were 5 feet or more in height with rare examples as tall as 6 feet. Between these extremes almost all possible heights were found.

The diameter of goldenrod stems varied with the luxuriance of the growth of the plants. Likewise, galls occurring on different parts of the stem, or on plants of different size, were found to vary in size with the varying thickness of the stems. The diameters of plant stems at points just below gall swellings ranged, in the 3,003 measured galls, from 2.3 to 10.8 mm., the average being 5.55 mm. (Table 1.)

Variations in the Galls

As a consequence of the range in size of plants and the various points of placement of galls upon the stems, galls were found at different heights above ground. Galls were usually found on the upper half of the goldenrod stalk, but this was influenced by the environment. They were frequently placed low on plants growing without much competition or without shading by other plants; but usually above the middle, or even terminal, on plants growing in competitive associations. Terminal galls examined in a lot of 1,000 amounted to 27.3 per cent. They were usually pear-shaped and ranged from 9 to 38 inches above the ground, the greater number being from 13 to 24 inches above the ground. The stem galls (72.7 per cent) were found from 6 to 36 inches above the ground with the greater number from 13 to 23 inches. They were usually spindle-shaped and placed below the crown of the plant.

Much variation in size and shape of galls was found. Of the 3,003 galls measured, no two were exactly alike. They varied in several respects, in the size of the gall, that is, in length, breadth, and interior capacity; in the position on the plant; and in the thickness and texture of the wall, some examples having pithy walls through which a pin could easily be inserted, whereas, on the other extreme, some were so woody that a pin could not be

TABLE 1. COMPARISON OF THICKNESS OF STEMS OF GOLDENROD PLANTS WITH THE SIZE OF GALLS THEY BORE AND THE SIZE OF SOME OF THE CONTAINED PUPÆ OF THE INSECT GALL MAKER

Diameter of stem just below gall	Number of examples	Average dimensions of gall (length by diameter)	Width of pupæ			
			Males		Females	
			Examples	Average width	Examples	Average width
Mm.		*Mm.*	*Number*	*Mm.*	*Number*	*Mm.*
2– 2.9	16	24.9 by 12.0	3	2.47	....	....
3– 3.9	286	28.3 by 13.3	58	2.69	44	2.97
4– 4.9	709	29.3 by 14.4	130	2.74	124	3.07
5– 5.9	909	30.4 by 15.2	191	2.77	179	3.09
6– 6.9	606	31.3 by 16.1	133	2.80	131	3.13
7– 7.9	308	33.3 by 16.9	77	2.82	62	3.15
8– 8.9	105	34.4 by 17.6	19	2.83	26	3.18
9– 9.9	55	35.2 by 18.1	10	2.82	10	3.21
10–10.9	9	36.8 by 19.8	1	....	2	3.27
Total	3,003	....	622	....	578	....

inserted at all. Some were linear, only a slight swelling of the stem indicating the presence of the gall insect. Others were globular, resembling the galls of the dipteron *Eurosta solidaginis* which occurred in association with *Gnorimoschema gallæsolidaginis,* but, incidentally, very rarely on the same plants. Most galls of *Gnorimoschema* were spindle-shaped, evidently typical of the species, whereas terminal galls were usually pear- or club-shaped. Extreme size and extreme shape—linear, spindle-shaped and globular—of the galls are illustrated in figure 3. Figure 4 shows a photograph of the various types.

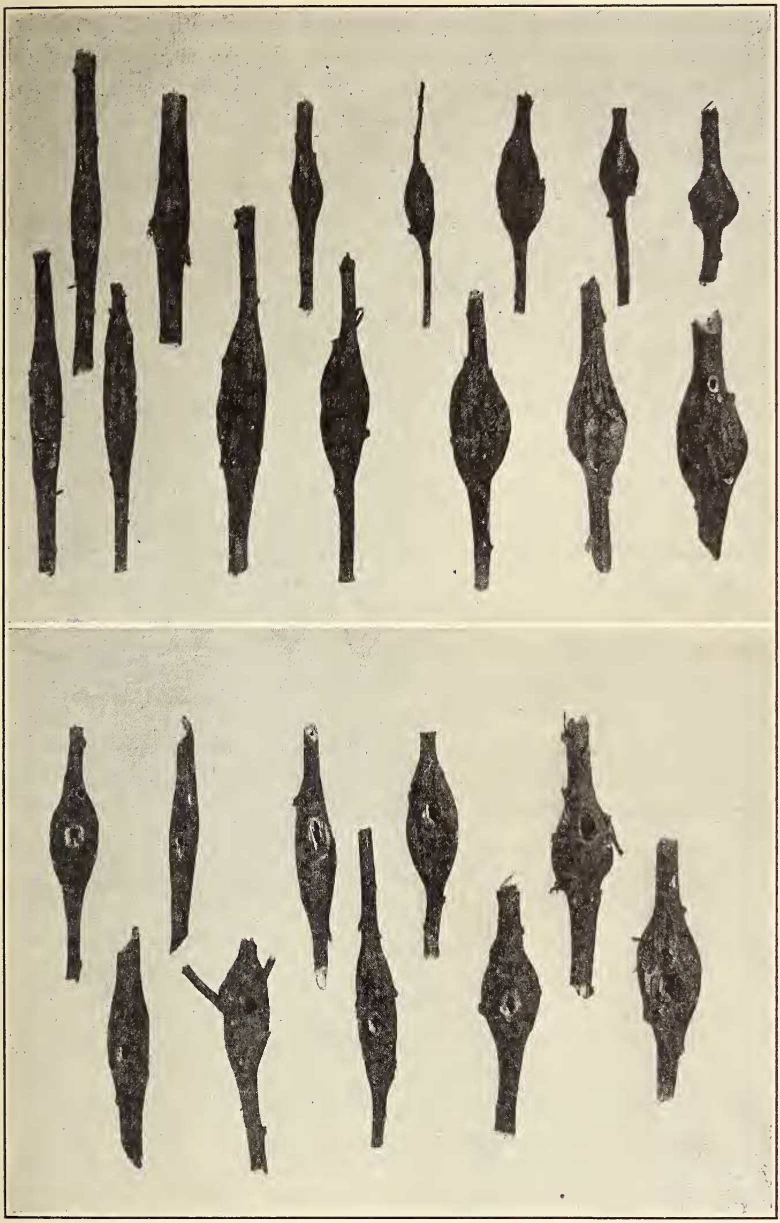
The galls ranged in length from 14 to 64 mm., and in thickness from 6 to 26 mm. The greater number, however, were between 24 and 35 mm. long and between 11 and 18 mm. in diameter.

Variations in the Insect Gall Makers

The variation in the size of the insect inhabitants of the galls could be conveniently ascertained by measuring the live pupæ. Of 1,200 measured pupæ, 622 males ranged in length from 7.9 to 12.0 mm. and in breadth from 2.05 to 3.30 mm., averaging 10.2 mm. long by 2.74 mm. broad. Similarly measured, 578 female pupæ ranged in length from 7.9 to 13.1 mm. and in breadth from 2.08 to 3.62 mm., averaging 11.4 mm. long by 3.11 mm. broad. One unique male pupa was found to be 5.6 mm. long by 1.5 mm. broad, much smaller than the smallest of the 622 male pupæ described above. In all of the above measurements the greater number of cases were grouped closely about the average.

Variations in the Emergence Plugs

The plugs that closed the emergence burrows varied somewhat in shape but most often were perfectly circular on both the inner and outer surfaces. They varied in diameter and in depth or thickness, and in the relationship of the two surfaces as to diameter. The inner surface was almost always of less diameter than the upper or outer surface; that is, the plugs were almost invariably "bungs" or stopper-shaped, and this difference between outer and inner diameters varied with the thickness of the plugs. The thickness of the plugs generally was dependent upon the thickness of the wall of the gall. In figure 5, extreme types of plug, as

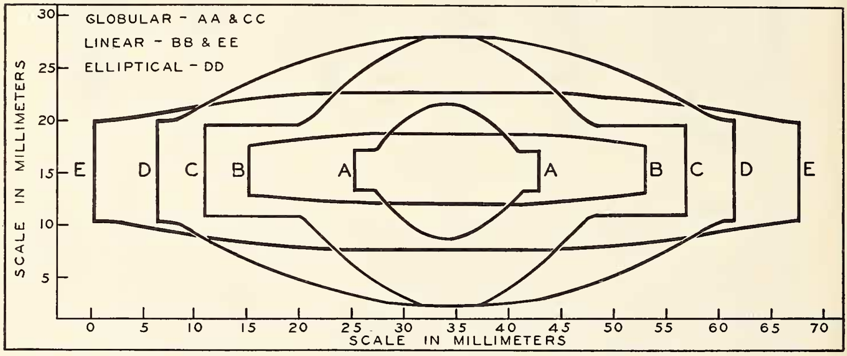


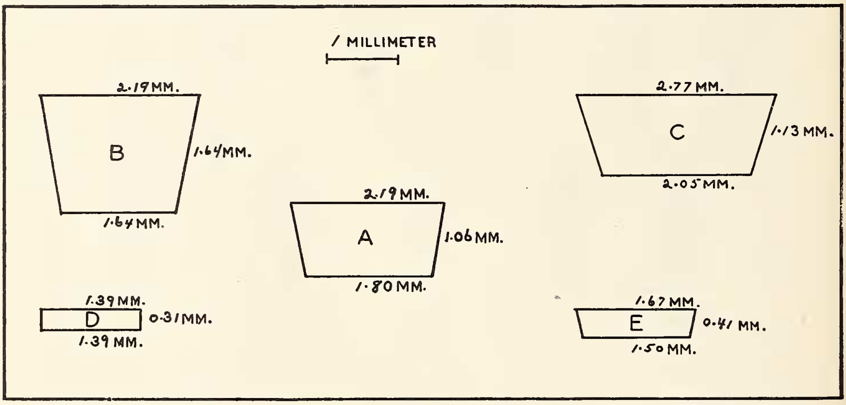
Above—FIGURE 4.—Various types of goldenrod galls. *Below*—FIGURE 6.—Goldenrod galls that have been attacked by birds.

well as an average plug, are illustrated. The outer diameter of 1,200 plugs ranged from 1.43 to 3.01 mm., by far the greater number being between 2 and 2.4 mm. Of 203 plugs that were completely studied, the upper surface ranged from 1.37 to 2.77 mm. (average 2.19) in diameter and the inner surface from 1.35 to 2.25 mm. (average 1.80). The thickness of the plugs ranged from 0.30 to 1.64 mm. (average 1.06). The difference between the outer and inner diameters of individual plugs ranged from 0.00 to 0.85 mm. (average 0.39).

DISCUSSION OF THE RELATIONSHIPS

It has been shown that the plants, the galls, and the insects inhabiting the galls all vary considerably in size, and it is the





Above—FIGURE 3.—Comparison of five extreme types of goldenrod galls. *Below*—FIGURE 5.—Types of plugs in goldenrod galls: A, average plug; B, extremely deep or thick plug; C, extremely wide plug; D, extremely small and unusual plug; E, thin plug of usual shape.

intention in the following paragraphs to show in what way the variation of the one is associated with the variation of the other.

Relationship of Diameter of Stem to Size of Gall

As previously noted, the diameter of the goldenrod stems immediately below the galls they bore ranged from 2.3 to 10.8 mm. Thus the largest stem observed was 4.7 times the diameter of the smallest. From field observations it seemed that small galls were usually found on small stems and large galls on large stems. This proved to be the case in 3,003 measured galls; in fact, it was found that the size of the galls increased in proportion to the stem diameter. A summary of the data is given in table 1. Plants were grouped into 9 size classes, according to stem diameter immediately below the galls, the size of the latter being averaged for each class. As shown in the table, the average gall size is larger proportionately as the stem diameter is greater, and the evidence indicates that, in general, a controlling factor in gall size is the diameter of the stem on which the gall is borne.

Relationship of Size of Pupa to Size of Gall

The range in breadth of pupæ was found to be from 2.05 to 3.31 mm. in males, and from 2.08 to 3.62 mm. in females, the pupæ occupying galls of various sizes. To determine whether the insects varied in proportion to the galls they inhabited, the former were arranged into 9 classes, according to breadth, the average size of galls inhabited by pupæ of each class being then determined. These data are given in table 2. In the case of each sex of the insect, it was found that the pupæ varied in breadth (here taken as a measure of size) proportionally to the size of the galls they inhabited, and it was indicated that a controlling factor in the size of the insect was the size of the gall which it inhabited or, very likely, the extent of the feeding area provided by the gall. Furthermore, female pupæ were on an average somewhat larger than male pupæ, as previously noted, and occupied on an average somewhat larger galls than the latter. Thus the average breadth of 578 female pupæ was 3.11 mm., while the average size of the galls they inhabited was 31.11 by 16.12 mm.; the average breadth of 622 male pupæ was 2.74 mm., and the average size of their galls was 28.87 by 15.23 mm.

TABLE 2. COMPARISON OF THE BREADTH OF PUPÆ OF THE INSECT GALL MAKER WITH SIZE OF THE GALLS THEY INHABITED AND THE DIAMETER OF THE EMERGENCE PLUGS OF THE GALLS

Breadth of pupæ in millimeters	Females				Males			
	Number of examples	Average size of galls		Average diameter of the plug	Number of examples	Average size of galls		Average diameter of the plug
		Length	Breadth			Length	Breadth	
		Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*
2.05–2.20	2	26.05	13.40	1.66	4	19.77	13.05	1.54
2.21–2.40	2	25.70	13.65	1.95	15	24.75	12.69	1.79
2.41–2.60	15	28.01	13.23	1.91	85	26.38	13.33	1.91
2.61–2.80	32	29.47	14.04	2.04	267	28.33	14.97	2.06
2.81–3.00	125	28.69	14.48	2.19	216	29.95	16.24	2.21
3.01–3.20	231	30.98	16.43	2.34	32	33.31	16.09	2.25
3.21–3.40	132	33.23	17.34	2.44	3	33.83	14.93	2.29
3.41–3.60	38	35.09	18.02	2.50	....	....	....	....
3.61–	1	40.30	18.80	2.84	....	....	....	....
Total	578	....	....	....	622	....	....	....
Average	....	31.11	16.12	2.31	....	28.87	15.23	2.09

Relationship of Size of Pupa to Diameter of Emergence Plug

To insure the free emergence of the moth from the gall it is necessary that an opening not only be prepared by the larva but that this opening be of suitable size, for if it is too small the moth will not be able to force itself through it. The size of the burrow and "plug" made by the insect are proportional to the size of the insect. This is shown in the data presented in table 2, and verified by placing 20 large pupæ in galls originally inhabited by small pupæ and sealing up the galls except for the emergence plugs, which were left undisturbed. Of these individuals, 1 pupa died, 18 gave rise to moths which died in the emergence burrow in their struggle for freedom, and 1 successfully emerged.

That suitable provision is made by the larvæ for moth emergence is shown by field examination of emerged galls, not a single example being found in which an adult had been unable to gain freedom by way of the emergence burrow. The relationship between the size of the burrow and the size of the insects may be a mere mechanical one, dependent upon the variation in the size of the larval mouthparts with larval size. At all events it was found that plug diameter varied directly with pupal size in each sex, and the size of the burrow was always such as to allow the escape of the adult moth. One unique male pupa was found to be only 1.5 mm. in breadth, and its emergence plug was 1.37 mm. in diameter.

Relationship of Diameter of Stem to Size of Pupa

Since the size of galls varies proportionately with the diameter of the stems of plants which bear them and the size of pupæ varies with the size of galls which they inhabit, it is obvious that the size of pupæ would vary proportionately with the diameter of the stems of plants bearing the galls they inhabit. This was found to be the case, as shown in table 1, in which the measurements of 1,200 pupæ are compared with data on gall size and plant-stem diameter.

PROTECTIVE VALUE OF THE GALL TO THE INSECT

While inhabiting the galls (that is, during the larval and pupal periods of the life cycle) more than half of the insects were destroyed by one means or another. It is apparent, therefore, that while the gall provides possible protection from some destructive agencies, it is not particularly effective against enemies which, in one way or another, have learned to gain access to the galls in order to feed upon the contained gall maker.

FATE OF THE INSECT GALL MAKER

Of 3,500 galls studied in the fall of 1929 only 46.7 per cent gave rise to moths. The most important single destructive agency was birds. Nearly as important as these was the combined attack by 6 species of parasites. Birds and parasites combined destroyed 35.9 per cent of the fall-examined galls and 35.9 per cent of spring-examined galls. Relatively few larvæ or pupæ were found to perish because of disease. A few galls were taken by leaf-cutting bees and ants; and a considerable number were attacked by insect predators, particularly predacious coleopterous larvæ, which were able, apparently, to lift out the protecting plug and to gain entrance into the interior of the gall through the emergence burrow. The fate of the insects is given in percentages in table 4.

BIRDS AS ENEMIES

Birds penetrated the galls and devoured the insect inhabitants in 18.7 per cent of fall-examined galls and in 20.9 per cent of spring-examined galls. They gained access through the tip of the gall, about the emergence burrow, in 11.8 per cent of the cases; through the base of the gall in 1.5 per cent; and in 86.7 per cent of the examples they gained access through the side of the gall, as shown in figure 6. Birds usually made their attack when the larvæ were full grown or after they had pupated, since in 76.9 per cent of the examples the emergence plugs had been formed, which, as has been shown, is the last act of the larva before pupation. In most of the remaining 23.1 per cent of bird-attacked galls the emergence burrows had been partly excavated, indicating that the larvæ were approximately full grown. In the fall of 1929 it appeared that the feeding by birds was limited to a period of a few weeks only, in September or early in October, when the larvæ were full grown, or nearly full grown, or after pupation had occurred; but the species of bird concerned was not determined. In general, only the largest galls were attacked by birds, perhaps because the larger stems that bore such galls afforded the firmer foothold needed by them in penetrating the galls.

Feeding by birds on this insect was general in the area studied, but not at all uniform in all localities, being found heavy in some spots, particularly in growths of large flourishing goldenrod plants, and very light in other spots. In other words, the heaviest bird feeding occurred in "pockets." In 35 collections of 100 galls each, the number penetrated by birds ranged from 1 to 48. In 9 collections, from 1 to 10 galls were attacked; in 17 collections, from 11 to 20; in 4 collections from 21 to 30; in 3 collections, from 31 to 40; and in 2 collections, between 41 and 48.

INSECT PARASITES AS ENEMIES

In the locality where these studies were made, six species of parasitic insects were found to attack *Gnorimoschema gallæsolidaginis,* usually in the larval stage. Three of these were important, and three were practically insignificant in importance; taken together, they accounted for but 17.26 per cent of 3,500 fall-examined galls. Each species of parasite is discussed briefly.

Copidosoma gelechiæ How.[2]

Copidosoma gelechiæ proved to be the most important insect parasite. The adult parasite oviposits in the host egg in the fall, according to Leiby.[3] In 94.9 per cent of galls containing larvæ parasitized by this species the emergence plugs had not been formed. This parasite develops polyembryonically, and a large number of parasites pack the body of the host larva, which is usually found to be swollen to several times its normal size when the parasites have pupated within its body. The parasite is usually found in the larger galls.

Of 100 larvæ from which adult parasites of *C. gelechiæ* emerged, 63 gave forth female parasites and 37 gave forth male parasites, the adult parasites from any one host larva being almost always of the same sex. Leiby[3] found that unfertilized eggs of this

[2] Determined by A. B. Gahan.

[3] Leiby, R. W., The polyembryonic development of *Copidosoma gelechiæ,* with notes on its biology. Jour. Morphology 37: 195–285. 1922.

parasite gave forth male adults and that fertilized eggs gave forth either male or female adults. In three instances noted by the writer a few males issued from larvæ giving forth large numbers of adult female parasites. In these cases more than one egg may have been laid by the adult parasite, or an egg by each of two adults may have been laid in such host eggs. Patterson[4] found similar cases which he attributed to this cause.

From the 100 parasitized host larvæ mentioned above, a total of 19,009 adult parasites emerged during the fall of 1929. Of these 13,427, or 70.63 per cent, were females; and 5,582, or 29.37 per cent, were males. The number of parasites emerging from a single larva varied greatly. In the case of female parasites the range in population per host was from 27 to 412; in the case of male parasites from 41 to 259 issued from host larvæ. Patterson,[4] in studying this parasite on *Gnorimoschema salinaris* Busck, found that the number of parasites per host in female broods, in 90 instances, ranged from 25 to 395, with an average of 198.48 individuals per host; and in male broods, in 62 instances, the range was from 41 to 345, the average being 175.32 individuals per host. Since, in the writer's investigations, the host larva that contained 27 parasitic pupæ appeared to be of approximately normal size, even including the parasites, or a little larger, the increase in larval bulk in the most heavily parasitized host larva—that containing 412 parasitic pupæ—appeared to be 15 times that of a normal larva. Of the female broods, in approximately half the cases, the parasitic population ranged from 100 to 250 per host, and nearly half of the male broods numbered from 100 to 200 per host.

The average number of female parasites per host larva was 213.1; the average number of male parasites per host larva was 150.9.

It was found that parasitized larvæ varied greatly in size and that this variability in size roughly paralleled a variability in gall size, a condition previously noticed in the pupæ of the gall insect and the galls in which they were found.

Although the populations of parasites per host larva were ex-

[4] Patterson, J. T., Observations on the Development of *Copidosoma gelechiæ*. Biol. Bul. 29: 333–372, illus. 1915.

tremely variable, no indication was found that competition for food among the parasites had at any time been keen. This is illustrated in the remarkable uniformity in size found in the adult parasites.

In order to determine variability in size of these parasites, the fore-wings of 10 specimens from each of the 100 host larvæ were measured. The average wing size of parasites emerging from individual host larvæ ranged from 1.33 to 1.72 mm. in the case of males, and from 1.31 to 1.62 mm. in the case of females. But it was when parasite size was studied in connection with parasite population groups that uniformity in parasite size was most noticeable. This is shown in table 3.

TABLE 3. MEAN SIZE OF FOREWING OF ADULT COPIDOSOMA GELECHIÆ FROM LARVÆ OF GNORIMOSCHEMA GALLÆSOLIDAGINIS HAVING THE VARIOUS PARASITE POPULATIONS INDICATED

Number of parasites per larva	Mean length of forewing of adult parasite	
	Females	Males
	Mm.	*Mm.*
1– 50	1.45	1.72
51–100	1.44	1.59
101–150	1.44	1.58
151–200	1.44	1.54
201–250	1.46	1.57
251–300	1.42	1.64
301–350	1.43	....
351–400	1.47	....
401–450	1.48	....

Adult male parasites were somewhat larger, on an average, than females, the average length of the fore-wing of 370 males being 1.56 mm., with three-fourths of the total falling between 1.51 and 1.71 mm. Of 630 females the average wing length was 1.43, with more than half falling between 1.37 and 1.51 mm. The populations of females in host larvæ were relatively larger than of males.

Calliephialtes notanda (Cress.)[5]

The second most important parasite, attacking 4.83 per cent of 3,500 fall-examined galls, was *Calliephialtes notanda*. Galls of all

[5] Determined by R. A. Cushman.

sizes were attacked by this parasite, but on the whole these galls were smaller than those attacked by *Copidosoma.* The adults of *Calliephialtes* emerged, with one exception, during the autumn. The female is provided with a long ovipositor, which she apparently is capable of inserting through the wall of the gall in order to reach the contained host insect. In 74 per cent of the observed instances, the host larva was able to complete the emergence burrow and plug before perishing. In the remaining 26 per cent of observed instances, the emergence plug had not been formed. When the larva of the parasite becomes full grown it forms a rather long, flat, brown-colored, leathery cocoon, which, in the cases observed, was peculiar in that it usually lay with the head of the parasite toward or even adjacent to the emergence burrow formed by the host larva for the escape of the moth; and it was by the burrow that the adult parasite usually escaped, although it is capable of gnawing its way through the wall of the gall when necessary. This species usually occurred singly, although in one instance two parasites were present. Although usually a primary parasite, it is sometimes a secondary, for in three instances adults emerged from cocoons of *Microgaster,* and one adult emerged from a host larva filled with pupæ of *Copidosoma.* It is able, apparently, to accommodate itself to whatever food may be available in the galls.

The adults of the parasite are extremely variable in size in each sex, although the males are usually smaller than the females. Size was judged in this case by measuring the length of the cocoon, for the reason that many parasites had issued before collections of material were made. The largest cocoon observed was 17.1 mm. long; the smallest, 6.8 mm. long. As was found to be the case with pupæ of the host insect, the variation of the parasite cocoons was comparable to variation in size of the galls in which they were found.

Microgaster gelechiæ Riley[6]

Microgaster gelechiæ was the third in importance as a parasitic enemy of the gall insect, attacking 4.40 per cent of 3,500 fall-examined galls. It was always found singly. The host larva gnaws the usual emergence burrow but rarely cuts an opening to

[6] Determined by A. B. Gahan.

the outside, leaving intact a portion of the wall of about the thickness of what would be the plug. When full grown the parasitic larva leaves the host larva and spins a cocoon of white silk, more or less fluffy in appearance; and in this, within the protecting gall, it passes the winter, emerging the succeeding spring. This parasite is more uniform in size than the preceding species, although varying somewhat, 60 per cent of the cocoons being from 6.7 to 6.9 mm. in length, the full range being from 6 to 7.3 mm.

Eurytoma bolteri Riley[7]

The fourth parasite in importance, attacking 1.29 per cent of 3,500 fall-examined galls, was *Eurytoma bolteri*. The parasitic larva feeds externally upon the larva or pupa of the gall insect, or upon other parasites. It was often found in galls parasitized by *Copidosoma,* in which case it devoured numbers of the pupæ of this parasite in the host larva, causing irregular devoured areas to appear in the inflated and rigid parasitized larva of the gall insect. This species occurred almost always singly per gall, and pupated without forming a cocoon. It was quite variable in size. Usually the adult parasites emerged in the fall, but a few remained in the galls over winter, emerging the following spring. It was usually found inhabiting smaller galls.

Tetrastichus sp.[8]

A small parasite, *Tetrastichus* sp., was found in only 18 out of 3,500 fall-examined galls, destroying 0.51 per cent of the gall insects. It attacks the pupæ exclusively, and the number of adult parasites emerging from a single pupa of the host ranged from 3 to 42. In certain instances adult parasites emerged in the autumn; in others, they passed the winter within the host pupæ, emergence of the parasites taking place the following spring. This species of parasite employs a unique method of gaining entrance into the galls. It gnaws its way in, but always through the emergence plug, thus choosing the one spot in the wall of the gall which is thinnest. Galls attacked by this parasite could easily be recognized by the small round entrance burrow of the parasite, usually at or near the center of the plug, but sometimes at its edge.

[7] Determined by A. B. Gahan.

[8] Determined by A. B. Gahan.

Microbracon furtivus (Fyles)[9]

The least important of the parasites, *Microbracon furtivus,* was represented in but 8 of 3,500 galls examined in the fall of 1929, thus being responsible for the death of 0.23 per cent of the gall insects. The number of parasites attacking individual gall insects was very variable, and their size varied according to population. From 3 to 22 of these parasites were found in individual galls, the average number of cocoons per gall being 8.1. This parasite attacks the larva of its host, and, when through feeding, the parasitic larvæ spin individual brown cocoons which are grouped about the inner wall of the gall at the base, just above the pile of excrement deposited by the gall insect. The cocoons adhere closely to the wall of the gall, and are inconspicuous, colored much like the wall and easily overlooked. The length of cocoons ranged from 2.6 to 6.1 mm., while the average length of cocoons in the various parasite populations per gall was as follows: With 3 cocoons per gall the average length was 5.6 mm.; 4 cocoons per gall, 4.78 mm.; 5 cocoons per gall, 4.92 mm.; 6 cocoons per gall, 4.45 mm.; while with 22 cocoons per gall they averaged 3.2 mm. in length. Females of this parasite have an ovipositor of sufficient length to be inserted through galls having medium thick walls. The insects pass the winter in the cocoons in the galls, the adult parasites emerging in the spring.

DISCUSSION OF PARASITISM

In the 35 collections of 100 galls each, made in the fall of 1929, each species of parasite (and parasitization as a whole) was quite differently represented. The extreme variation in occurrence of the several species and the parasitization in general, and also other causes of death, are given in table 4. Parasites, both in general and specifically, occurred more numerously in "pockets" in the field, a condition heretofore observed in the case of bird feeding. Four species of parasites were clearly larval parasites, although one, when pressed for food, fed on competing parasites; one was strictly a pupal parasite; while one was an indiscriminate feeder, being able to subsist on larvæ or pupæ of the gall insect, or on other parasites. On the whole, of 604 parasitized galls examined, relatively few showed competition among these parasites.

[9] Determined by A. B. Gahan.

TABLE 4. FATE OF INSECT GALL MAKER AT RICHMOND, VA., 1929–30

	Moths issued	Taken by birds	Destroyed by insect parasites							Larvae died of disease	Pupae died	Galls taken by bees or ants	Destroyed by insect predators, or fate unknown
			Total parasitism	*Copidosoma gelechiæ*	*Calliephialtes notanda*	*Microgaster gelechiæ*	*Eurytoma bolteri*	*Tetrastichus* sp.	*Microbracon furtivus*				
	Per cent	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*	*Per cent*
Fall of 1929 examinations, 3,500 galls	46.75	18.69	17.26	6.00	4.83	4.40	1.29	0.51	0.23	3.38	0.80	0.63	12.49
Spring of 1930 examinations, 234 galls	42.74	20.94	14.96	2.57	6.41	2.99	0.85	....	2.14	3.42	2.13	....	15.81
Greatest percentage in any one collection of 100 galls	76.00	48.00	28.00	13.00	16.00	11.00	6.00	....	2.00	9.00	8.00	2.00	23.00
Least percentage in any one collection of 100 galls	19.00	1.00	7.00	1.00	0.00	0.00	0.00	....	0.00	0.00	0.00	0.00	1.00

Of the two larval parasites which occurred several to a gall, and populations of which differed greatly in different galls, one was shown to suffer little variation in the size of adult parasites, as between small and large populations, while the second showed considerable variation in the size of individuals when present in various numbers.

The sizes of the galls in which the several parasites were found were, on the average, somewhat different. Except for *Copidosoma,* which occupied large galls, the parasites were found in galls smaller, on an average, than the general average of gall size. The average sizes of the galls, the insect inhabitants of which met various fates, is given in table 5, in which this matter is made clear.

TABLE 5. COMPARISON OF THE SIZE OF GALLS, THE INSECT MAKERS OF WHICH MET VARIOUS FATES*

Description of fate of the insect gall maker	Number of examples	Average size of galls	
		Length	Breadth
		Mm.	*Mm.*
Galls containing pupae	1,200	29.95	15.67
Galls containing female pupae	578	31.11	16.12
Galls containing male pupae	622	28.87	15.23
Galls attacked by birds and parasites	1,084	31.97	15.17
Galls attacked by birds	592	33.96	15.98
Galls attacked by parasites	492	29.62	14.19
Copidosoma gelechiæ	121	34.09	15.72
Calliephialtes notanda	169	28.53	13.81
Microgaster gelechiæ	152	28.02	13.73
Eurytoma bolteri	43	26.55	13.15
Microbracon furtivus	7	32.19	13.41
Galls attacked by predators, or fate unknown, etc.	719	30.02	15.21
General average of all galls	3,003	30.69	15.37

* Some 500 galls were examined for fate and discarded before measurements were undertaken.

When the larva of the gall insect becomes full grown it lays down a sheet of silk on the inner wall of the gall. The effect is to waterproof the gall, a condition to which the various parasites appear to be adapted. Parasites kept indoors in glass vials stoppered with cotton hibernated under quite dry conditions; yet they passed the hibernating period perfectly, as did certain guests of the gall insect, notably leaf-cutting bees. Moisture during hibernation was certainly not necessary in these cases, nor for that matter was it necessary for the pupæ of the host insect or fall-emerging parasites, which were kept under similar conditions for shorter periods.

INSECT PREDATORS

A number of the gall insects were destroyed by miscellaneous enemies and these have been grouped with those whose fate was unknown. Predacious larvæ of Carabidæ and Lampyridæ were found in certain galls, and they probably had devoured the gall-making insect. These larvæ, having strong mandibles, were apparently able to pry out the emergence plug and so gain entrance to the galls, and they were found only in galls in which the emergence plugs had been formed.

Two species of ants were occasionally found in galls. They had devoured the pupa of the gall insect or its parasites, and very likely were also able to pry off the emergence plug, being found only in galls in which this structure had been formed. A number of mites were often found running over the pupa of the gall insect, but these may not have been enemies.

INSECT GUESTS

The insect guests of the gall maker were of two kinds, those that used the galls while they were still occupied by the gall-making insect and those that used the deserted galls. Among the former may be mentioned leaf-cutting bees, that excavated an opening into the gall, in which they constructed one or more of their leaf-covered brood cells. Goldenrod stalk borers (larvæ of Coleoptera) that, in gnawing through the stalk, enter the galls and feed therein were frequently seen. The empty galls, from which moths had emerged or that had been attacked by birds or parasites, served as snug retreats for hosts of small spiders during the winter. From these deserted galls were also collected species of small Hemiptera and Coleoptera representing several families, as well as hibernating thrips and ants.

SUMMARY

In the foregoing paper the writer discusses the probable cause of the gall formation produced in goldenrod by *Gnorimoschema*

gallæsolidaginis, the habits of the insect gall maker, the variation found in plants, galls, and insects (both host and parasites), the causes of this variation, and the efficiency of the gall in affording protection for the insect occupants from natural enemies.

The study was carried on at Richmond, Va., in 1929, and consisted of examinations of 3,500 galls.

From measurements it was found that the size of the insect gall maker varied with the size of the galls. The size of the latter varied with the luxuriance of growth of the goldenrod plants, and growth of plants varied in turn with numerous ecological factors, such as type and fertility of soil, exposure of plants to light, and competition of goldenrod plants with others of the same or other species. Ultimately it appeared that the size which the insect gall makers attained depended in general upon the conditions under which the infested plants grew.

Descriptions are given of the remarkable means which the larva of the gall insect provides for the escape, and at the same time the protection, of the moth. This is the making of a "stopper" or "bung" to the previously and otherwise completely walled gall, which is the last act of the larva of the gall insect before pupating. This stopper is so constructed that, while the merest pressure from within will force it out and open the passage through which the moth can escape, it can hardly be forced in by pressure directed on it from the exterior.

Birds, probably woodpeckers, proved to be the most important enemy of the gall insect, taking the insects from 18.69 per cent of the galls examined in the fall of 1929. Parasites were collectively only slightly less important as enemies, being responsible for the death of 17.26 per cent of the host insects at the same time. The insect parasites noted were of 6 species, the most numerous species destroying 6 per cent and the least numerous species taking 0.23 per cent of the insect gall makers. In the cases of some of these parasites, it is shown that the individuals varied in size with the size of the galls they inhabited, and consequently with the size of the host larvæ, which provided them with a greater or a lesser amount of food.